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Marine Geology 242 (2007) 39 – 63

MARINE GEOLOGY
INTERNATIONAL JOURNAL OF MARINE GEOLOGY, GEOCHEMISTRY AND GEOPHYSICS

www.elsevier.com/locate/margeo

Modern distribution of salt marsh foraminifera and thecamoebians in the Seymour–Belize Inlet Complex, British Columbia, Canada

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Accepted 31 August 2006

Abstract

Foraminifera and thecamoebian distribution along two marsh transects, in the Waump (WIR 16) and Wawwat'l (WIR 12) Indian Reserves, in the Seymour–Belize Inlet Complex, north coastal British Columbia were investigated. Based on Q- and R-mode cluster analysis of the faunal distributions three high abundance, low diversity faunal assemblages were identified; the Freshwater, Brackish and High Salt Marsh Assemblages. The Freshwater Assemblage is dominated by the soil thecamoebian species *Cyclopyxis kahli*, a significant presence of centropyxids and *Nebela collaris*. The Brackish Assemblage is characterized by abundant centropyxids and less than 10% foraminifera. The High Salt Marsh Assemblage is characterized by the dominance of *Balticammina pseudomacrescens*.

The results of this study show the high potential of combined thecamoebian/foraminifera analyses for paleo-sea level research under lower salinity marsh conditions.

Keywords: marsh foraminifera; thecamoebians; salt marsh; Seymour–Belize Inlet

1. Introduction

Reconstruction of Holocene sea level change in coastal environments has primarily been based on biological proxies as indicators of paleo-elevation (e.g. Devoy, 1979; Shennan, 1982; Long and Innes, 1993; Gehrels et al., 1996; Goldstein and Watkins, 1998). Foraminifera, diatoms and thecamoebians (testate amoebae) have been demonstrated to be particularly useful as they not only form coastal marsh communities that are closely linked to elevation relative to mean sea level and local tidal regimes but preserve well in the fossil record (e.g. Horton, 1999; Gehrels et al., 2001; Patterson et al., 2005). If the modern elevational ranges of these communities are known with some precision, then the presence of in situ fossil

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doi:10.1016/j.margeo.2006.08.009

assemblages can be used as proxies for paleo-elevation with higher accuracy than a reconstruction based on sedimentological evidence alone (van de Plassche, 1986). The precision of any derived paleo-sea level reconstructions is therefore heavily dependant on studies of the present day vertical zonation of microscopic communities in salt marshes (Patterson et al., 2005).

The purpose of the present study is to determine the elevational distribution of marsh foraminifera and thecamoebians in two salt marshes found within the Seymour–Belize Inlet Complex (SBIC), a previously unstudied portion of the British Columbia mainland coast located more than 450 km to the north of the Fraser River Delta, the closest mainland site previously examined (Fig. 1; Williams, 1989; Patterson, 1990; Jonasson and Patterson, 1992; Williams, 1999). Transects were examined from the Waump Indian Reserve 16 Marsh, located at the head of Alison Sound, and from the Wawwat'l Indian Reserve 12 Marsh, at the upper end of Seymour Inlet (Fig. 1). As there are no nearby previously studied marshes from which to develop a transfer function training set (e.g., Gehrels, 2000; Edwards et al., 2004; Patterson et al., 2004; Horton and Edwards, 2006), the results presented here will provide a critical baseline for planned future paleo-sea level reconstruction in the area.

1.1. Previous work

Past research on elevation controlled salt marsh communities along the Pacific coast of North America has focused primarily on foraminifera (e.g. Patterson, 1990; Guilbault et al., 1995; Scott et al., 1996; Ozarko et al., 1997; Patterson et al., 1999, 2000, 2005; Tobin et al., 2005) and diatoms (e.g. Nelson and Kashima, 1993; Hemphill-Haley, 1995; Nelson et al., 1996; Patterson et al., 2000, 2005).

The first study that examined marsh foraminiferal faunas in British Columbia was a cursory examination of a limited number of samples from a few localities around the province by Phleger (1967) with no further research carried out until Williams (1989) completed a study on the Fraser Delta. Williams (1989) identified three well defined elevational zones within the intertidal area, with the highest zone being almost entirely comprised of *Jadammina macrescens* (Brady and Robertson, 1870), but misidentified as *Polystomammina grisea* (Earland, 1934), found in the high marsh, *Ammonia beccarii* (Linné, 1758) dominant in a narrow mid marsh zone, and a low marsh zone dominated by *Miliammina fusca* (Brady and Robertson, 1870). In a follow-up larger-scale study on the Fraser Delta, Patterson (1990) identified six distinct assemblages that were controlled by elevation, salinity and organic content of the sediment. These included two high marsh zones that were distinguished based on salinity differences. In lower salinity areas close to the Fraser River, *J. macrescens* dominated the high marsh assemblage, while higher salinity areas of the high marsh were dominated by a mixture of *J. macrescens* and *Trochammina inflata* (Montagu, 1808). Mid elevational areas of the marsh were variably rich in *A. beccarii*, and *Cribroelphidium gunteri* (Cole, 1931), and the low marsh was dominated by *M. fusca*. The Fraser Delta contains the only marshes in British Columbia identified thus far that have significant populations of calcareous species present. In a third study of the Fraser Delta marsh foraminiferal faunas, Jonasson and Patterson (1992) recognized that there was a significant difference in the foraminiferal faunas found at the surface of the marsh and those in the immediate subsurface. They attributed these changes to the influence of the infaunal habitat of some species and taphonomic processes.

Guilbault et al. (1995) estimated the amount of coastal subsidence due to past earthquakes near Tofino (west coast of Vancouver Island) using marsh foraminifera. As in previous studies, these researchers recognized a high marsh assemblage dominated by *J. macrescens*, whereas the low marsh was dominated by *M. fusca*. The boundary between these two zones was defined as the point where the dominance shifted from one species to the other. Thecamoebians were present in small quantities in the High Marsh, and their numbers were noted to increase until they dominated in supratidal areas.

Ozarko et al. (1997) found that the marsh at Nanaimo, southeastern Vancouver Island was also characterized by *J. macrescens* in the high marsh and *M. fusca* in low marsh areas. These researchers determined that there were quantifiable differences between the surface foraminiferal distribution (top cm) and that found in the subsurface that were related to the infaunal habitat of some marsh foraminiferal species as well as post mortem taphonomic factors. Ozarko et al. (1997) suggested that potential difficulties associated with correlating modern (0–1 cm) surface samples that have not been taphonomically impacted, and that do not include infaunally dwelling species with biased subsurface samples might be corrected for by utilizing a slightly thicker surface sample, in paleo-sea level studies. Additional taphonomic studies were continued in Zeballos' marsh, on the north-west coast of Vancouver Island, to further examine the issue of whether thicker surface samples should be used in paleo-sea level research to provide a better analog of subsurface

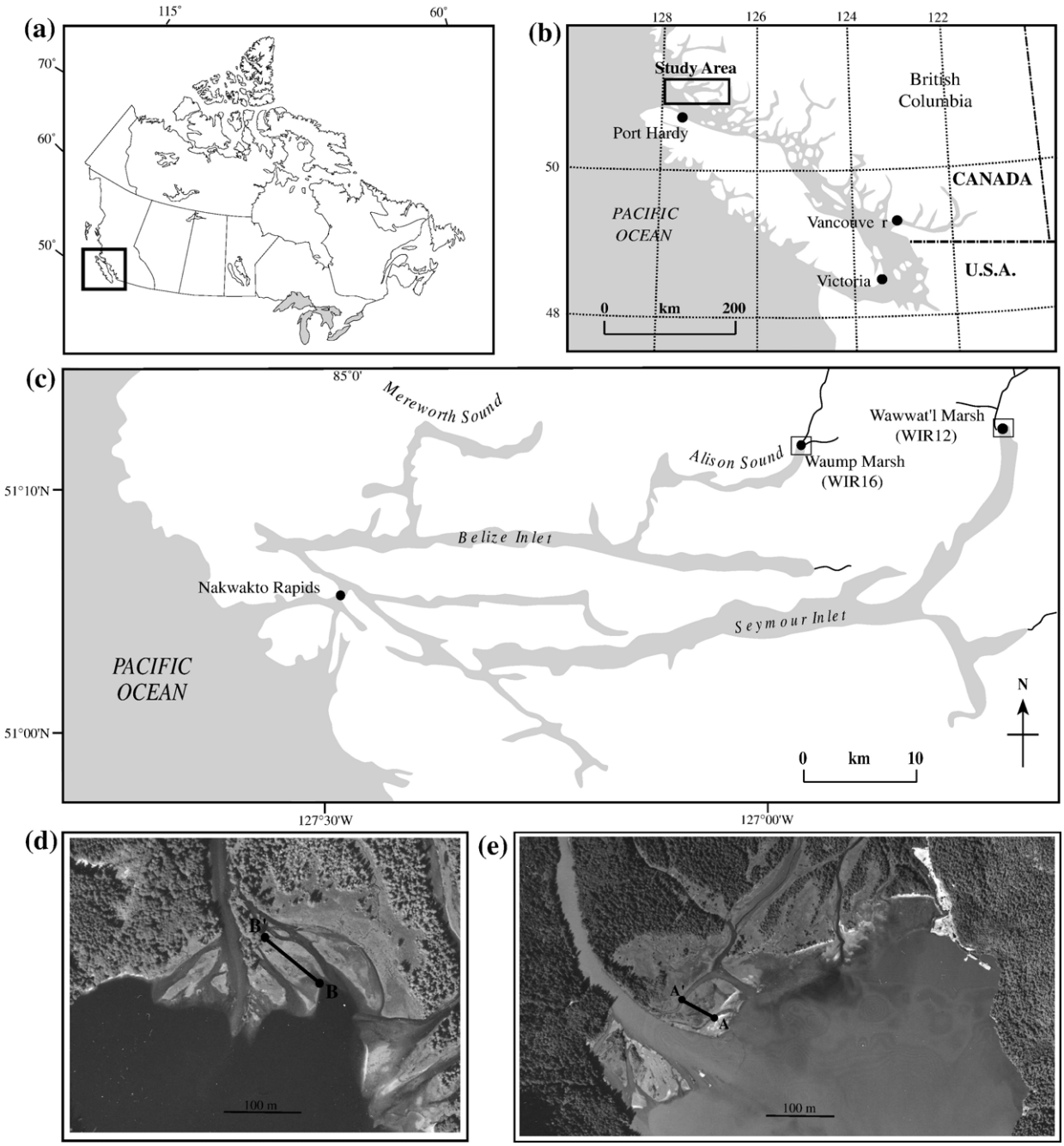


Fig. 1. (a) Map of Canada. (b) Map of Vancouver Island and mainland coastal British Columbia. (c) Map of the Seymour-Belize Inlet Complex, with sampling sites Waump (WIR16) Marsh and Wawwat'l (WIR12) Marsh. (d) Aerial photograph of the Waump Indian Reserve 16 (WIR16) Marsh, located at the head of Alison Sound, indicating the position of the sampled transect. (e) Aerial photograph of the Wawwat'l Indian Reserve 12 (WIR12) Marsh, located at the head of Seymour Inlet, indicating the position of the sampled transect.

conditions (Patterson et al., 1999). The high marsh at the Zeballos site was dominated by *J. macrescens* and *Balticammina pseudomacrescens* Brönnimann, Lutze, and Whittaker, 1989. The distribution of foraminifera in the high marsh here was not considerably different from that reported in previous studies. However, this was the first study in the region to differentiate between the morphologically similar *J. macrescens* and *B. pseudomacrescens*. A middle marsh fauna was also recognizable at Zeballos, dominated by *B. pseudomacrescens* and *M. fusca*. As at

other British Columbia localities *M. fusca* characterized the low marsh (Patterson et al., 1999). Tobin et al. (2005) utilized the Nanaimo dataset of Ozarko et al. (1997) and the Zeballos dataset of Patterson et al. (1999) to carry out a non-statistical reassessment of the influence of infaunal habitat on the subsurface makeup of foraminiferal faunas. Despite the presence of an often large and mobile living infaunal foraminiferal population moving amongst variably preserved subfossil assemblages, they concluded that the impact of these biasing factors need not be considered when utilizing marsh foraminiferal data in paleo-sea level studies.

Most recently a large-scale study at Zeballos used comparative proxy records derived from foraminifera, diatoms and macrophytes to determine that higher resolution paleo-sea level curves could be derived when using a multiproxy approach (Patterson et al., 2000, 2005).

1.2. Study site

The SBIC is comprised of a network of deep, steep-sided glacial fjords that is typical of much of the northern coast of British Columbia. The area is densely vegetated by a temperate rain forest and is almost devoid of human presence.

The SBIC is characterized by a marine west coast climate that is controlled by variations in Northeast Pacific atmospheric and oceanic circulation, particularly the seasonally dominant Aleutian Low in winter, and North Pacific High in summer (Ware and Thomson, 2000). The SBIC opens to Queen Charlotte Sound via the very narrow, 300 m wide Nakwakto Rapids, the only link with the ocean (Fig. 1). The bottleneck at Nakwakto Rapids, unnavigable except at slack tide, results in the development of strong ebb and flood tides, which

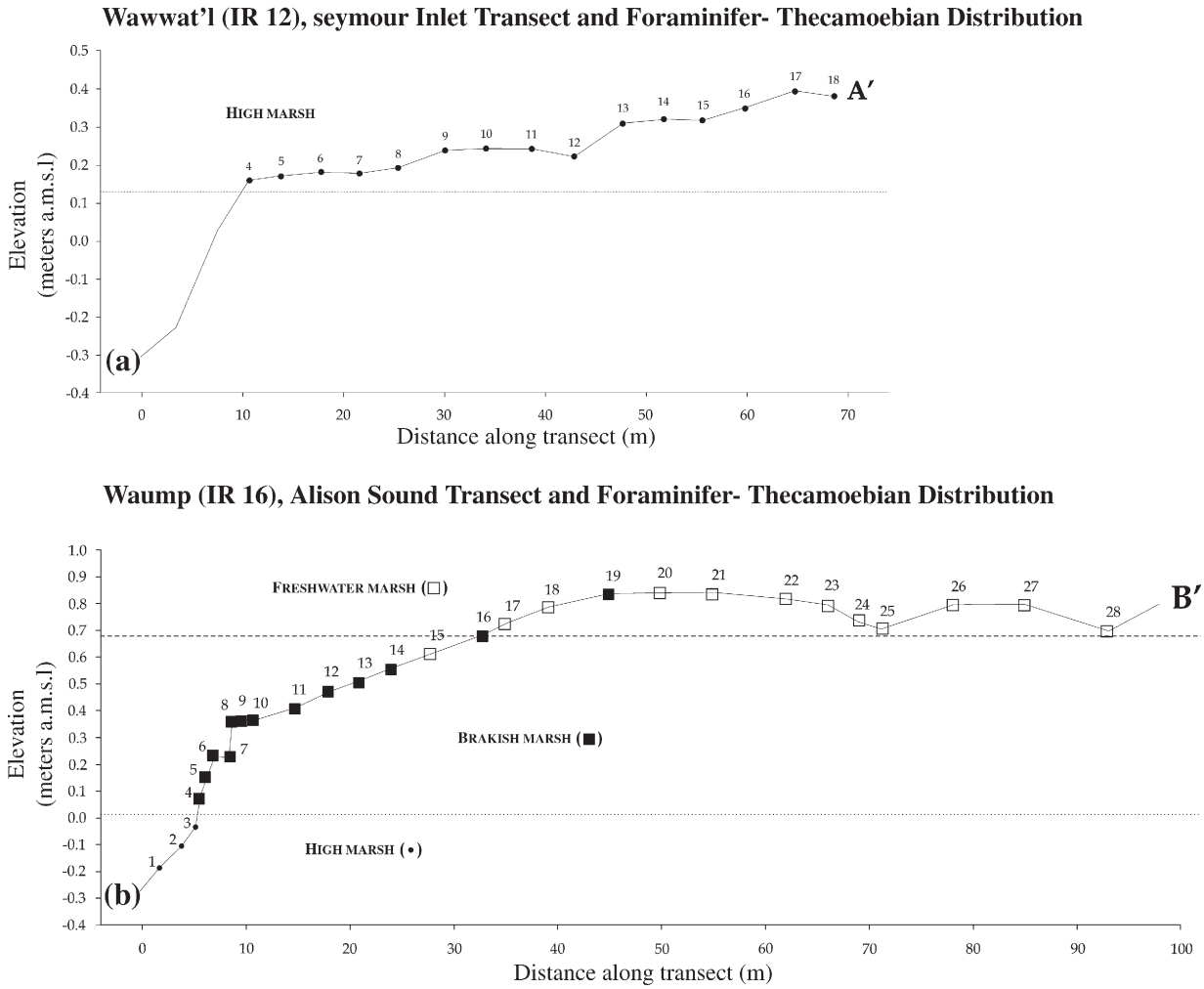


Fig. 2. Transects across the WIR12 and the WIR 16 marshes, showing position of the samples and elevation in meters above mean sea level relative to mean tide level.

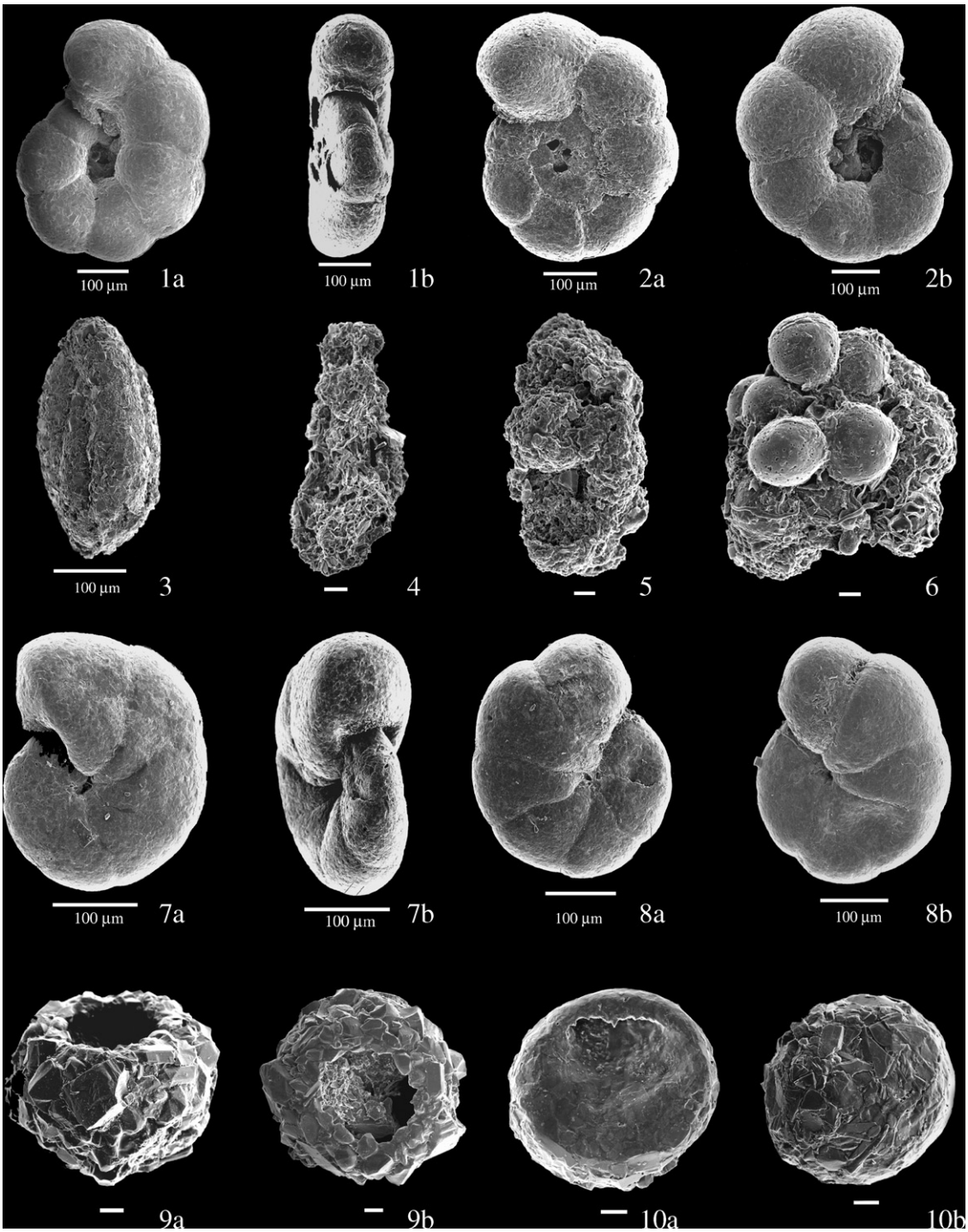
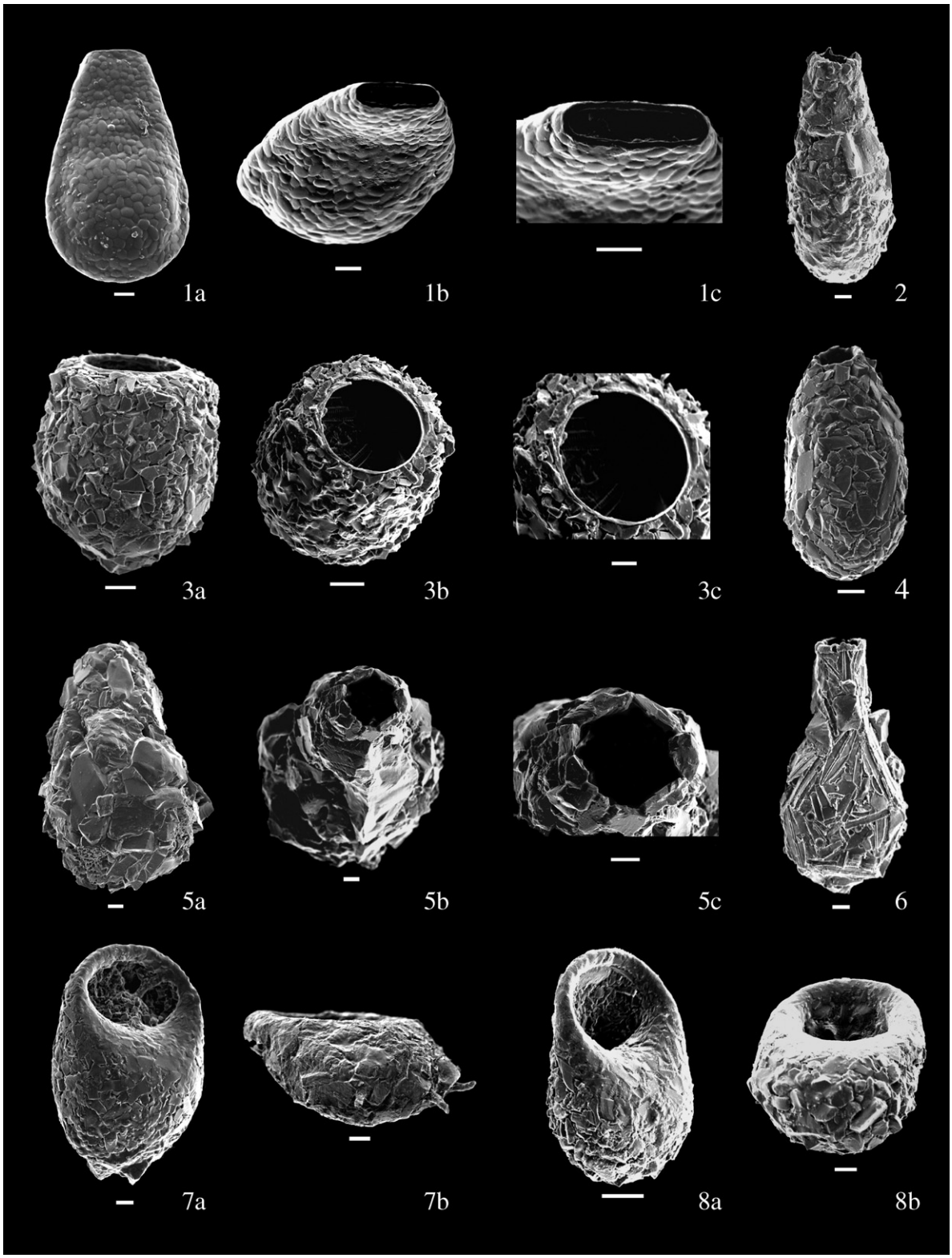


Plate I. 1–2. *Balticammina pseudomacrescens* Brönniman, Lutze and Whittaker, 1989. 1a, side view of one specimen. 1b, apertural view of the same specimen. 2a, side view of a second specimen showing supplementary apertures. 2b, other side of the second specimen. 3. *Miliammina fusca* (Brady, 1870), side view. 4–5. *Polysaccammina ipohalina* Scott, 1976. 4, side view of specimen one. 5, side view of specimen two. 6. *Hemisphaerammina bradyi* Loeblich and Tappan, 1957, view of specimens attached to debris. 7–8. *Haplophragmoides manilaensis* Anderson, 1953. 7a, side view of specimen one. 7b, apertural view of the same specimen showing the aperture. 8a, 8b, both sides of a second specimen showing great symmetry. 9. *Cyclopyxis kahli* (Deflandre, 1929). 9a, side view of specimen showing coarse agglutination. 9b, apertural view of the same specimen showing circular centered aperture. 10. *Centropyxis aculeata* Ehrenberg, 1832 strain 'discoides' Reinhardt et al., 1998. 10a, apertural view. 10b, dorsal view of the same specimen. Scale bars are 10 µm unless otherwise noted.


1a
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7b
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average between 5 and 9 knots. The large volume of water entering the SBIC at flood tide cannot be drained fast enough by water exiting the complex through the Nakwakto Rapids during ebb tide (Thomson, 1981). The result is a considerable difference in tidal range, which varies from 4.5 m in Queen Charlotte Sound to only 1.3 m in the SBIC. This imbalance, together with freshwater input from rivers and creeks within the SBIC, results in the development of brackish conditions in the surface waters at the head of the inlets.

2. Methods

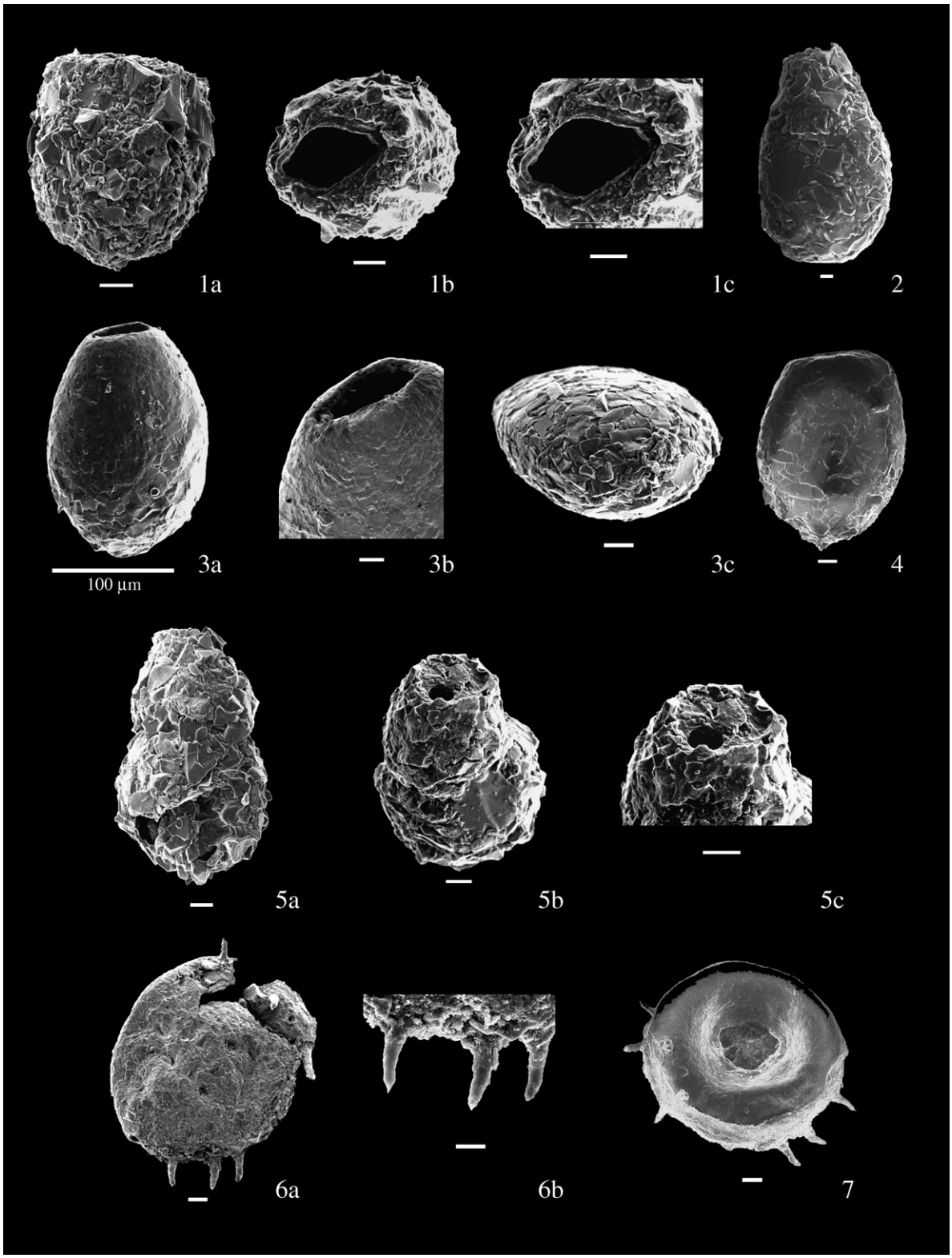
Forty-eight short-cores were collected from transects across the Waump (WIR16) and Wawwat'l (WIR12) marshes by shore parties from the CCGS *Vector* in April 2002. Positions of sample stations and relative elevations along transects were determined by using a differential GPS and total station Electronic Distance Measuring Device (EDM), with reference to elevation of the highest tide level (Waump marsh) or the lowest tide level (Wawwat'l marsh) occurring on the day of fieldwork. The GPS readings of the tide levels were subsequently converted to meters relative to mean tide level (MTL) based on the observed tidal heights calculated by the Canadian Hydrographic Service for Frederick Sound and Alison Sound (Canadian Hydrographic Service, 2002), and are given here as meters above mean sea level (m amsl).

Thirty short cores were collected along a 98 m transect across the WIR16 marsh, while 18 cores were collected along a 68 m transect across the WIR12 marsh (Fig. 2). Upon return to the laboratory aboard the CCGS *Vector*, all cores were treated with isopropyl alcohol as a preservative and refrigerated at 4 °C in sealed plastic bags. The samples were then shipped to laboratory facilities at Carleton University, where they were stored at 3.5 °C in a cold room, until subsampled for analysis in January 2005.

Forty-eight 10 cm^3 aliquots from the uppermost 3 cm of the cores were selected for this study. This sampling strategy was chosen as a compromise based on recent results in marshes in Vancouver island and elsewhere (e.g., Patterson et al., 1999; Horton and Edwards, 2006). The use of a 3 cm depth avoids both the taphonomic bias that arises from analyzing only the first cm of surface samples, and the time-consuming task of analyzing thicker (10 cm) samples. Samples were disaggregated using a Burrell wrist action shaker for 1 h and left overnight to settle. All samples were then sieved using a 35-mesh Tyler (500 μm) screen to remove coarse organic material, and a 230-mesh Tyler (63 μm) screen to retain thecamoebians and foraminifera. Samples were not stained with Rose Bengal as the two and a half years between collection of the cores and subsampling was considered too long an interval to expect an accurate assessment of living foraminiferal and thecamoebian protoplasm. The samples were subsequently divided into aliquots for quantitative analysis using a wet splitter (after Scott and Hamelin, 1993), and examined under an Olympus SZH10 stereo microscope. Scanning electron photomicrographs of foraminifera and thecamoebians were obtained using a JEOL 6400 Scanning Electron Microscope at the Carleton University Research Facility for Electron Microscopy (CURFEM). These digital images were converted into plates using Adobe © Photoshop 7.0 (Plates I II III).

Conductivity and pH measurements were not made in the field due to equipment malfunction. Determination of conductivity and pH values for both marshes were obtained following transport of the sediments to Carleton University conforming to the procedure typically applied to soils (Rowell, 1994). Conductivity data were transformed into salinity values through application of the Practical Salinity Scale of 1978, using the UNESCO/John Hopkins University calculator (UNESCO, 1985) (Table 1). The organic content of the samples was calculated using the loss-on-ignition (LOI) technique. Samples were air-dried for 24 h at 45 °C and subjected to combustion at 550 °C for 4 h. The organic matter content was calculated as percentage of weight loss of the dried samples after combustion (Yu et al., 2003). Aliquots of the samples were treated with 30% hydrogen peroxide to remove organic content prior

Plate II. 1. *Nebela collaris* Ehrenberg, 1848. 1a, side view of specimen showing test made of idiosomes. 1b, apertural view of the same specimen showing flatness of the test and keel. 1c, detail of the aperture of the same specimen. 2. *Difflugia oblonga* Ehrenberg, 1832 strain 'tenuis' Reinhardt et al., 1998, side view. 3. *Difflugia urceolata* Carter, 1864 strain 'urceolata' Reinhardt et al., 1998. 3a, side view showing coarse agglutination. 3b, apertural view of the same specimen showing lip around the aperture. 3c, detail of the aperture. 4. *Difflugia oblonga* Ehrenberg, 1832 strain 'lanceolata' Reinhardt et al., 1998, side view showing tapering towards the aperture. 5–6. *Difflugia oblonga* Ehrenberg, 1832 strain 'oblonga' Reinhardt et al., 1998. 5a, side view of specimen. 5b, apertural view of the same specimen. 5c, detail of aperture. 6, side view of a specimen with test made of diatom frustules, probably *Frustulia* sp. 7. *Centropyxis constricta* Ehrenberg, 1843 strain 'constricta' Reinhardt et al., 1998. 7a, apertural view showing angled aperture and basal spines. 7b, side view of the same specimen showing well rounded fundus and spines. 8. *Centropyxis constricta* Ehrenberg, 1843 strain 'aerophila' Reinhardt et al., 1998. 8a, apertural view showing aperture in a 45° angle. 8b, view of the same specimen showing lack of spines. Scale bars are 10 μm.


1a
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2
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100 μm
3b
3c
4
5a
5b
5c
6a
6b
7

to particle size analysis. Mechanical dispersion by ultrasonic stirring was used to separate the sediment particles. The particle size was determined using a laser particle size analyzer (GALAI CIS-100) to the 99% confidence level. Details of the results of LOI and grain size analysis can be found in Doherty (2005).

3. Analysis and results

Five agglutinated foraminiferal species and 18 thecamoebian taxa were identified in the samples collected from the two marshes. The relative fractional abundance (F_i) of each taxonomic unit for each sample was calculated as follows:

$$F_i = \frac{C_i}{N_i}$$

where C_i is the species counts and N_i is the total of all the species counts in that sample. Using this information, standard error (S_{xi}) associated with each taxonomic unit was calculated using the following formula:

$$S_{xi} = 1.96\sqrt{\frac{F_i(1-F_i)}{N_i}}$$

If the calculated standard error was greater than the fractional abundance for a particular species in all samples then that species was not included in successive multivariate analyses (Patterson and Fishbein, 1989). Five foraminifera and 17 thecamoebian species were found in statistically significant numbers in at least one sample, with the thecamoebian *Pontigulasia compressa* (Carter, 1864) being removed from ensuing multivariate data analysis.

The 48 samples quantified were also assessed to determine which ones were statistically significant. The probable error (pe) for each of the total sample counts was calculated using the following formula:

$$\mathrm{pe} = 1.96\left(\frac{s}{\sqrt{X_i}}\right)$$

where s is the standard deviation of the population counts and X_i is the number of counts at the station being investigated. A sample was judged to have a statistically significant population (SSP) if the total counts obtained for each taxon were greater than the pe (Boudreau et al., 2005). A total of 47 sediment samples were deemed to have SSP counts: 29 from WIR16 marsh and 18 from WIR12 marsh. The void sample M19-S0 from WIR16 marsh was the only sample discarded and not included in subsequent multivariate analysis (Patterson and Fishbein, 1989).

The Shannon–Weaver diversity index (SDI) was used to assess environmental stability based on the proportion and diversity of species found at each sample station within the marshes. This index was calculated using the Shannon and Weaver (1949) formula:

$$\mathrm{SDI} = -\sum_{l}^{S}\left(\frac{F_i}{N_i}\right) \times \ln\left(\frac{F_i}{N_i}\right)$$

where S is equal to the species richness of the sample. Environments are considered to be stable if the SDI falls between 2.5 and 3.5, in transition between 1.5 and 2.5, and stressed between 0.1 and 1.5 (Patterson and Kumar, 2002). Low values are also typical in ecotone environments such as salt marshes where harsh conditions severely limit the number of species found there (Patterson et al., 2005). Results indicate a transitional environment in both WIR16 marsh, where the SDI ranged from 1.56 to 2.16, and WIR12 marsh, where it varied between 1.43 and 2.13 (Table 2). Since the SDI is dependent upon the number of species identified on the study, the use of a 63 μm sieve may have influenced the result through loss of specimens, or even of species. However, a more detailed study of the smaller fraction of the samples is intended, that will clarify this issue and determine which species, if any, are being lost by the use of a coarser mesh.

R-mode cluster analysis was used to determine which species were most closely associated with others and thus best characterized a particular assemblage (Fishbein and Patterson, 1993). Q-mode cluster analysis was used to group statistically similar populations using Ward's Minimum variance, and recorded as squared-Euclidean distances (Fishbein and Patterson, 1993). Q-mode and R-mode cluster analyses were carried out on the five

Plate III. 1. *Difflugia oblonga* Ehrenberg, 1832 strain 'glans' Reinhardt et al., 1998. 1a, side view of specimen showing absence of neck. 1b, apertural view of the same specimen. 1c, detail of aperture. 2. *Pontigulasia compressa* Carter, 1864, showing characteristic V-shape compression in base of neck. 3–4. *Heleopera sphagni* (Leidy, 1874). 3a, side view of specimen showing characteristic increase in grain size towards the fundus. 3b, detail of the elongated, narrow aperture. 3c, view of the fundus showing flatness of the test. 4, side view of another specimen showing less variation in grain size. 5. *Lagenodifflugia vas* (Leidy, 1874). 5a, side view of specimen showing characteristic constriction at base of the neck. 5b, apertural view of the same specimen. 5c, detail of aperture. 6–7. *Centropyxis aculeata* Ehrenberg, 1832 strain 'aculeata' Reinhardt et al., 1998. 6a, dorsal view of broken specimen showing basal spines. 6b, detail of spines in the same specimen. 7, apertural view of another specimen showing aperture and spines. Scale bars are 10 μm unless otherwise noted.

Table 1
Values of altitude (m amsl, relative to mean tide level), pH, conductivity (μS/cm) and salinity (psu) for the sediment samples from WIR12 and WIR16

Sample	Altitude (m amsl)	pH	Conductivity (μS/cm)	Salinity (‰)	Assemblage
M30-S1	−0.31	5.1	990	7.04	Outliers
M30-S2	−0.23	5.9	592	4.05	
M30-S3	0.03	6.1	691	4.78	
M30-S4	0.16	5.3	640	4.41	High marsh
M30-S5	0.17	5.5	853	5.1	
M30-S6	0.18	5.1	1193	8.61	
M30-S7	0.17	5.5	867	6.1	
M30-S8	0.19	5.7	839	5.89	
M30-S9	0.24	5.7	1325	9.64	
M30-S10	0.24	5.5	1849	13.85	
M30-S11	0.25	5.5	491	3.32	
M30-S12	0.22	5.5	745	5.19	
M30-S13	0.31	5.9	761	5.31	
M30-S14	0.32	5.5	1339	9.75	
M30-S15	0.31	5.6	704	4.88	
M30-S16	0.35	5.3	909	6.42	
M30-S17	0.39	5.4	790	5.52	
M30-S18	0.38	5.7	696	4.82	
M19-S1	−0.26	6.2	485	3.28	
M19-S2	−0.16	5.6	559	3.81	
M19-S3	−0.09	5.5	527	3.58	
M19-S4	− 0.02	5.5	327	3.81	Brackish
M19-S5	0.09	5.4	427	3.58	
M19-S6	0.17	5.1	319	2.16	
M19-S7	0.24	5.9	235	2.86	
M19-S8	0.22	5.8	319	2.1	
M19-S9	0.36	5.8	366	1.52	
M19-S10	0.37	6	228	2.27	
M19-S11	0.42	6	403	1.85	
M19-S12	0.48	5.9	386	1.09	
M19-S13	0.51	6.3	176	2.69	
M19-S14	0.56	5.9	345	2.57	
M19-S15	0.62	6	303	1.12	Freshwater
M19-S16	0.69	6.1	252	2.28	Brackish
M19-S17	0.73	5.5	350	2.32	Freshwater
M19-S18	0.79	5.2	452	3.04	
M19-S19	0.84	6.9	154	0.97	Brackish
M19-S20	0.84	5.9	271	1.77	Freshwater
M19-S21	0.85	6.3	163	1.03	
M19-S22	0.82	5.7	429	2.88	
M19-S23	0.8	5.6	256	1.66	
M19-S24	0.74	5.7	306	2.01	
M19-S25	0.71	5.9	242	1.57	
M19-S26	0.8	6	310	2.04	
M19-S27	0.7	6.1	182	1.16	
M19-S28	0.8	6.8	270	1.76	

foraminifera and 18 thecamoebian species in the 47 samples from WIR16 and WIR12 (Fig. 3), and organized into a hierarchical diagram of the combined dataset (Boudreau et al., 2005).

Preliminary Q and R-mode analyses, and subsequent visual inspection, indicated that sample M19-S29 from WIR16 and samples M30-S1, M30-S2 and M30-S3 from WIR12 were anomalous outliers, and as such were removed from the database prior to final cluster analysis. The anomalous samples from WIR12 were from the most seaward and lowest elevational section of WIR12 (−0.31 and −0.03 m amsl, Fig. 2). The faunas in these samples were deemed to have probably been transported, most likely the result of wave action or seasonal flooding of the adjacent stream. This faunal assemblage was comprised of a mixture of species characteristic of both salt and freshwater marshes, but in unusual proportions (25% foraminifera, 25% centropyxids, 25% *Cyclopyxis kahli* (Deflandre, 1929), 8.25% of *Difflugia oblonga* strains, and several other thecamoebian species). The foraminifera *B. pseudomacrescens* (range 0–23%, average 8.4%) and *M. fusca* (range 2.4–15.0%, average 7.3%) were present, but in proportions not really typical of any part of a salt marsh, and in conjunction with the soil indicator thecamoebian *C. kahli* (range 18.8–34.1%, average 25.4%), a species uncommon at such a low elevation.

Further evidence of reworking at these stations was provided by sedimentological analysis, which indicated that these samples were primarily comprised of medium to coarse-grained sand with a very high proportion of heavy mineral particles. The samples also had very low organic matter content when compared to the other samples examined from both marshes, all of which were organic rich with abundant plant debris. The elevational gradient at these stations is also quite steep when compared with the rest of the profile, going from −0.31 m amsl to 0.16 m amsl in a distance of less than 10 m, suggesting that these stations may be prone to wave and current action (Fig. 2).

Multivariate analyses were then carried out on the reduced dataset. The hierarchical cluster analysis results indicated the existence of three distinct elevation controlled assemblages, with all present in WIR16, but only one in WIR12 (Fig. 3). These assemblages characterize high salt marsh to brackish/freshwater environments, and are differentiated based on the relative abundances of *B. pseudomacrescens* and thecamoebian species.

Canonical Correspondence Analysis (CCA) was conducted on the dataset to examine the relationships between the faunal distribution and certain environmental variables using the program CANOCO 4 (ter Braak and Smilauer, 1998). This ordination method was used to explore which of the following environmental factors: elevation, sediment type, pH, conductivity and organic content (LOI) is most closely correlated with the faunal distribution. CCA is an efficient ordination

technique when species have bell-shaped response curves with respect to environmental gradients (Birks, 1995).

The results of the CCA plotted along two axes that account for 23% of the total variance in the faunal data (Fig. 4). The unexplained (77%) of the total variance may be due to other factors (e.g. variations in the sites of transects) that are not considered in the analysis. It could also be due to a large amount of stochastic variation. The explained percentage is, however, similar to other biological variables that have a large number of samples with zero values (Zong and Horton, 1999). The first axis, with an eigenvalue of 0.131, correlates moderately (r^2 = 0.57) with conductivity, but negatively with elevation. The second axis, defined by an eigenvalue of 0.045, relates the fauna to substrates, and is positively correlated (r^2 = 0.766) with clay and silt, and negatively with sand. Therefore, axis 2 reflects a grain size gradient from clay to silt through to sand fractions.

On the basis of conductivity and elevation, CCA distinctively delineated the faunal distributions into freshwater/brackish water and high marsh settings, providing reinforcing evidence for the hierarchical cluster groupings derived by cluster analysis.

3.1. Freshwater Assemblage

The Freshwater Assemblage is only present in WIR16, and includes samples 15, 17, 18, and 20 to 28. The average salinity within this assemblage is very low, with a mean of only 1.9‰ (range 1.0–3.0‰). This assemblage is overwhelmingly dominated by thecamoebians. As would be expected in an essentially freshwater environment, foraminifera comprise only a minor, probably transported, component of the observed fauna, with *B. pseudomacrescens* found at 0.5% in a single sample, and *M. fusca* found at 1.1% in another sample.

This assemblage characterizes a narrow elevational range in the highest part of the marsh examined (0.62–0.84 m amsl, Fig. 2). The most abundant species is the thecamoebian *C. kahli* (range 22.6–37.9%, average 28.8%). The centropyxids *Centropyxis aculeata* 'aculeata' (Reinhardt et al., 1998) (range 13.0–34.6%, average 21.4%) and *C. aculeata* 'discoides' (Reinhardt et al., 1998) (range 2.7–18.0%, average 8.64%) also comprise a dominant component of the assemblage. *Heleopera sphagni* (Leidy, 1874) (range 0–16.1%, average 9.3%), as well as *D. oblonga* 'oblonga' (Reinhardt et al., 1998) (range 0–10.2%, average 4.9%), *Centropyxis constricta* 'constricta' (Reinhardt et al., 1998) (range 0–36.4%, average 8.5%) and *C. constricta* 'aerophila' (Reinhardt et al., 1998) (range 0–13.2%, average 5.5%) are also present but in reduced numbers when compared with their occurrence in the Brackish Assemblage. *Nebela collaris* (Ehrenberg, 1848) reaches its highest abundance in this assemblage (range 2.2–17.8%, average 8.5%).

CCA grouped together the species of this assemblage, and that of the underlying brackish-water (e.g. *C. aculeata* "aculeata", *C. aculeata* "discoides", *H. sphagni*, *C. kahli*, *D. oblonga* "oblonga" and *N. collaris*).

3.2. Brackish Assemblage

The Brackish Assemblage is also only present in WIR16, samples 4 to 14 and samples 16 and 19 (0.09 and 0.84 m amsl, Fig. 2) and was characterized by an average salinity of 2.3‰ (range 1.0–2.9‰). This assemblage is dominated by thecamoebians, with foraminifera comprising less than 10% of observed fauna. The abundant occurrence of thecamoebians *C. aculeata* 'aculeata' (range 10.3–29.7%, average 20.5%) and *C. aculeata* 'discoides' (range 4.0–29.3%, average 17.2%) define this assemblage, although the thecamoebians *H. sphagni* (range 6.8–19.3%, average 14.0%), *C. kahli*, (range 4.3–19.5%, average 9.1%), and *D. oblonga* 'oblonga' (range 2.1–13.5%, average 6.2%) are important subsidiary species. Two other species of centropyxids, *C. constricta* 'aerophila' and *C. constricta* 'constricta' are also notable assemblage components (range 4.3–23.6, average 12.0%; and range 0–20.3%, average 6.8%, respectively). Two foraminiferal species were found to be present in this assemblage, *B. pseudomacrescens* and *M. fusca*. Only *B. pseudomacrescens* was of any relative significance though, with an average abundance of 8.1% (range 0–23.8%).

3.3. High Salt Marsh Assemblage

The High Salt Marsh Assemblage contains the three lowermost examined samples from WIR16 marsh (samples 1 to 3) and all the samples from WIR12 marsh included in the cluster analysis (samples 4 to 18) (Fig. 2). The samples from WIR16 are below the mean low tide level (−0.02–(−0.17) m amsl), whereas WIR12 is slightly higher (0.16–0.39 m amsl). The observed salinity for the assemblage averaged 6.1‰ but ranged from 3.3‰ to a maximum of 13.8‰.

The dominant species in this assemblage is the foraminifera *B. pseudomacrescens*, which ranged in abundance from 14.1% to 51.8% (average of 30.9%). *C. kahli* was also important, averaging 16.7% of the fauna (range 0–27.9%). Centropyxids are present as well in sizeable numbers, with significant occurrences of *C. constricta* 'aerophila' (range 4.2–29.2%, average 14.0%), *C. constricta* 'constricta'

Table 2
Taxonomic unit counts, probable error, Shannon–Weaver diversity index, fractional abundances and standard error for sediment samples from WIR12 and WIR16

Sample	M19-S1	M19-S2	M19-S3	M19-S4	M19-S5	M19-S6	M19-S7	M19-S8	M19-S9
Taxonomic counts	327	362	281	292	277	291	288	378	368
Probable error	41.0	39.0	44.3	43.4	44.6	43.5	43.7	38.2	38.7
Shannon–Weaver diversity	2.13	1.73	1.66	1.85	1.90	1.86	1.96	1.86	1.95
Height above mean sea level (m)	− 0.17	− 0.09	− 0.02	0.09	0.16	0.24	0.22	0.36	0.37
Balticammina pseudomacrescens	0.165	0.431	0.292	0.250	0.238	0.220	0.128	0.005	0.019
Standard error ±	0.040	0.051	0.053	0.050	0.050	0.048	0.039	0.007	0.014
Centropyxis aculeata “aculeata”	0.061	0.091	0.075	0.240	0.245	0.230	0.299	0.111	0.122
Standard error ±	0.026	0.030	0.031	0.049	0.051	0.048	0.053	0.032	0.033
Centropyxis constricta “aerophila”	0.174	0.061	0.221	0.045	0.043	0.062	0.056	0.235	0.147
Standard error ±	0.041	0.025	0.048	0.024	0.024	0.028	0.026	0.043	0.036
Centropyxis constricta “spinosa”	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008
Standard error ±	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009
Centropyxix aculeata “discoides”	0.162	0.130	0.210	0.113	0.126	0.134	0.115	0.267	0.293
Standard error ±	0.040	0.035	0.048	0.036	0.039	0.039	0.037	0.045	0.047
Centropyxix constricta “constricta”	0.110	0.110	0.000	0.000	0.000	0.000	0.000	0.095	0.141
Standard error ±	0.034	0.032	0.000	0.000	0.000	0.000	0.000	0.030	0.036
Cyclopyxis kahli	0.000	0.000	0.000	0.045	0.054	0.069	0.104	0.045	0.052
Standard error ±	0.000	0.000	0.000	0.024	0.027	0.029	0.035	0.021	0.023
Difflugia bacillariarum	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Difflugia oblonga “glans”	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Difflugia oblonga “lanceolata”	0.107	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.034	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Difflugia oblonga “oblonga”	0.040	0.022	0.060	0.051	0.058	0.069	0.135	0.122	0.106
Standard error ±	0.021	0.015	0.028	0.025	0.027	0.029	0.040	0.033	0.031
Difflugia oblonga “spinosa”	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Difflugia oblonga “tenuis”	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Difflugia protaeiformis “accuminata”	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
Difflugia urceolata “urceolata”	0.095	0.000	0.142	0.000	0.000	0.007	0.000	0.000	0.000
Standard error ±	0.032	0.000	0.041	0.000	0.000	0.009	0.000	0.000	0.000
Difflugia urens	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Haplophragmoides malinaensis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Heleopera sphagni	0.000	0.000	0.000	0.192	0.181	0.186	0.118	0.095	0.068
Standard error ±	0.000	0.000	0.000	0.045	0.045	0.045	0.037	0.030	0.026
Hemisphaerammina bradyi	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lagenodifflugia vas	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Miliammina fusca	0.055	0.110	0.000	0.003	0.014	0.017	0.014	0.021	0.005
Standard error ±	0.025	0.032	0.000	0.007	0.014	0.015	0.014	0.015	0.008
Nebela collaris	0.000	0.000	0.000	0.062	0.040	0.007	0.031	0.000	0.038
Standard error ±	0.000	0.000	0.000	0.028	0.023	0.009	0.020	0.000	0.020
Polysaccammina ipohalina	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pontigulasia compressa	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard error ±	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

M19-S10	M19-S11	M19-S12	M19-S13	M19-S14	M19-S15	M19-S16	M19-S17	M19-S18	M19-S19	M19-S20	M19-S21	M19-S22
371	394	559	1330	1288	1191	619	818	746	891	349	698	419
38.5	37.4	31.4	20.4	20.7	21.5	29.8	26.0	27.2	24.9	39.7	28.1	36.3
2.05	2.00	1.99	1.78	2.03	1.91	1.95	1.92	2.07	2.16	1.91	2.01	1.70
0.37	0.41	0.47	0.51	0.56	0.62	0.69	0.73	0.79	0.84	0.84	0.84	0.82
0.092	0.030	0.057	0.005	0.009	0.002	0.003	0.005	0.003	0.000	0.000	0.000	0.000
0.029	0.017	0.019	0.004	0.005	0.002	0.004	0.005	0.004	0.000	0.000	0.000	0.000
0.226	0.249	0.188	0.251	0.199	0.188	0.207	0.137	0.130	0.103	0.201	0.165	0.232
0.043	0.043	0.032	0.023	0.022	0.022	0.032	0.024	0.024	0.020	0.042	0.028	0.040
0.113	0.117	0.102	0.357	0.061	0.099	0.134	0.108	0.099	0.090	0.103	0.132	0.021
0.032	0.032	0.025	0.026	0.013	0.017	0.027	0.021	0.021	0.019	0.032	0.025	0.014
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.003	0.019	0.006	0.090	0.005
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.004	0.009	0.008	0.021	0.007
0.146	0.122	0.225	0.040	0.249	0.181	0.226	0.108	0.130	0.185	0.109	0.110	0.064
0.036	0.032	0.035	0.011	0.024	0.022	0.033	0.021	0.024	0.026	0.033	0.023	0.024
0.154	0.203	0.025	0.036	0.077	0.018	0.063	0.013	0.024	0.086	0.011	0.039	0.000
0.037	0.040	0.013	0.010	0.015	0.008	0.019	0.008	0.011	0.018	0.011	0.014	0.000
0.043	0.099	0.136	0.099	0.117	0.246	0.118	0.351	0.261	0.195	0.309	0.246	0.379
0.021	0.029	0.028	0.016	0.018	0.024	0.025	0.033	0.032	0.026	0.048	0.032	0.046
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.058	0.013	0.000	0.003	0.024
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.017	0.008	0.000	0.004	0.015
0.070	0.023	0.016	0.046	0.021	0.037	0.011	0.035	0.021	0.076	0.040	0.040	0.093
0.026	0.015	0.010	0.011	0.008	0.011	0.008	0.013	0.010	0.017	0.021	0.015	0.028
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.034	0.059	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.012	0.017	0.000	0.000	0.000	0.000
0.003	0.008	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000
0.005	0.009	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.039	0.000	0.007	0.000
0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.013	0.000	0.006	0.000
0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.001	0.000
0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.003	0.002	0.000	0.003	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.116	0.104	0.193	0.107	0.143	0.161	0.160	0.145	0.161	0.162	0.109	0.149	0.064
0.033	0.030	0.033	0.017	0.019	0.021	0.029	0.024	0.026	0.024	0.033	0.026	0.024
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.018	0.003	0.046	0.020	0.044	0.000	0.005	0.012	0.014	0.000	0.000
0.000	0.000	0.011	0.003	0.011	0.008	0.016	0.000	0.005	0.007	0.012	0.000	0.000
0.005	0.030	0.004	0.001	0.001	0.002	0.000	0.000	0.000	0.000	0.011	0.000	0.000
0.007	0.017	0.005	0.001	0.002	0.002	0.000	0.000	0.000	0.000	0.011	0.000	0.000
0.032	0.015	0.036	0.051	0.077	0.045	0.034	0.022	0.044	0.013	0.086	0.017	0.117
0.018	0.012	0.015	0.012	0.015	0.012	0.014	0.010	0.015	0.008	0.029	0.010	0.031
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.002	0.000	0.000	0.000

(continued on next page)

Table 2 (*continued*)

M19-S23	M19-S24	M19-S25	M19-S26	M19-S27	M19-S28	M19-S29	M30-S1	M30-S2	M30-S3	M30-S4	M30-S5	M30-S6
312	306	616	314	305	368	297	190	220	273	401	692	926
42.0	42.4	29.9	41.9	42.5	38.7	43.1	53.8	50.0	44.9	37.1	28.2	24.4
1.68	1.68	1.71	1.68	1.56	1.61	1.99	1.05	1.13	1.82	1.53	1.75	2.03
0.80	0.73	0.71	0.80	0.80	0.70	0.80	− 0.31	− 0.23	0.03	0.16	0.17	0.18
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.231	0.486	0.371	0.227
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.049	0.036	0.027
0.346	0.310	0.295	0.204	0.184	0.185	0.145	0.342	0.355	0.073	0.035	0.043	0.062
0.053	0.052	0.036	0.045	0.043	0.040	0.040	0.067	0.063	0.031	0.018	0.015	0.015
0.026	0.010	0.034	0.000	0.000	0.035	0.273	0.000	0.000	0.000	0.042	0.094	0.119
0.018	0.011	0.014	0.000	0.000	0.019	0.051	0.000	0.000	0.000	0.020	0.022	0.021
0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.007	0.006
0.006	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.006	0.005
0.045	0.075	0.029	0.086	0.072	0.027	0.111	0.116	0.136	0.015	0.105	0.246	0.202
0.023	0.030	0.013	0.031	0.029	0.017	0.036	0.045	0.045	0.014	0.030	0.032	0.026
0.000	0.000	0.000	0.245	0.364	0.307	0.118	0.000	0.000	0.040	0.060	0.065	0.130
0.000	0.000	0.000	0.048	0.054	0.047	0.037	0.000	0.000	0.023	0.023	0.018	0.022
0.279	0.278	0.323	0.229	0.226	0.321	0.158	0.516	0.468	0.341	0.192	0.108	0.159
0.050	0.050	0.037	0.046	0.047	0.048	0.042	0.071	0.066	0.056	0.039	0.023	0.024
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.003
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.004
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
0.016	0.026	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.014	0.018	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.077	0.062	0.102	0.054	0.010	0.033	0.027	0.000	0.000	0.059	0.015	0.030	0.029
0.030	0.027	0.024	0.025	0.011	0.018	0.018	0.000	0.000	0.028	0.012	0.013	0.011
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.003	0.000	0.005	0.037	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.006	0.000	0.008	0.021	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.003	0.011	0.000	0.000	0.000	0.000	0.005	0.001	0.018
0.000	0.000	0.000	0.000	0.006	0.011	0.000	0.000	0.000	0.000	0.007	0.003	0.009
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
0.131	0.088	0.057	0.000	0.056	0.000	0.037	0.000	0.000	0.000	0.007	0.014	0.009
0.037	0.032	0.018	0.000	0.026	0.000	0.021	0.000	0.000	0.000	0.008	0.009	0.006
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.044	0.000	0.001	0.002
0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.024	0.000	0.003	0.003
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.041	0.150	0.047	0.014	0.018
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.023	0.026	0.042	0.021	0.009	0.009
0.077	0.147	0.131	0.178	0.075	0.076	0.094	0.000	0.000	0.048	0.000	0.001	0.002
0.030	0.040	0.027	0.042	0.030	0.027	0.033	0.000	0.000	0.025	0.000	0.003	0.003
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

M30-S7	M30-S8	M30-S9	M30-S10	M30-S11	M30-S12	M30-S13	M30-S14	M30-S15	M30-S16	M30-S17	M30-S18
507	936	917	755	982	1831	375	311	452	1452	1119	689
33.0	24.3	24.5	27.0	23.7	17.3	38.3	42.1	34.9	19.5	22.2	28.3
1.88	1.91	1.90	2.01	1.99	2.13	1.81	1.28	1.45	1.87	1.93	1.82
0.17	0.19	0.24	0.24	0.25	0.22	0.31	0.32	0.31	0.35	0.39	0.38
0.304	0.322	0.277	0.303	0.257	0.205	0.360	0.453	0.518	0.234	0.223	0.141
0.040	0.030	0.029	0.033	0.027	0.018	0.049	0.055	0.046	0.022	0.024	0.026
0.148	0.098	0.132	0.057	0.086	0.115	0.051	0.003	0.020	0.070	0.074	0.052
0.031	0.019	0.022	0.017	0.017	0.015	0.022	0.006	0.013	0.013	0.015	0.017
0.087	0.135	0.160	0.132	0.066	0.104	0.163	0.167	0.104	0.193	0.211	0.292
0.025	0.022	0.024	0.024	0.016	0.014	0.037	0.041	0.028	0.020	0.024	0.034
0.002	0.000	0.000	0.026	0.021	0.027	0.005	0.000	0.011	0.014	0.007	0.003
0.004	0.000	0.000	0.011	0.009	0.007	0.007	0.000	0.010	0.006	0.005	0.004
0.150	0.122	0.110	0.098	0.174	0.122	0.064	0.071	0.055	0.055	0.110	0.060
0.031	0.021	0.020	0.021	0.024	0.015	0.025	0.028	0.021	0.012	0.018	0.018
0.047	0.092	0.064	0.148	0.077	0.097	0.091	0.003	0.035	0.098	0.137	0.087
0.018	0.019	0.016	0.025	0.017	0.014	0.029	0.006	0.017	0.015	0.020	0.021
0.178	0.159	0.183	0.148	0.238	0.235	0.187	0.264	0.217	0.278	0.182	0.279
0.033	0.023	0.025	0.025	0.027	0.019	0.039	0.049	0.038	0.023	0.023	0.033
0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
0.000	0.000	0.000	0.000	0.006	0.003	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.005	0.002	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.001	0.005	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.002	0.003	0.000	0.000	0.000	0.000	0.000	0.000
0.045	0.037	0.045	0.016	0.017	0.017	0.029	0.006	0.002	0.015	0.009	0.019
0.018	0.012	0.013	0.009	0.008	0.006	0.017	0.009	0.004	0.006	0.006	0.010
0.000	0.002	0.001	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.003	0.002	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.019	0.011	0.022	0.016	0.006	0.000	0.000	0.007	0.000
0.000	0.000	0.000	0.010	0.007	0.007	0.013	0.009	0.000	0.000	0.005	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.018	0.005	0.009	0.005	0.007	0.017	0.013	0.003	0.009	0.009	0.012	0.029
0.011	0.005	0.006	0.005	0.005	0.006	0.012	0.006	0.009	0.005	0.006	0.013
0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.008	0.004	0.007	0.019	0.021	0.015	0.016	0.023	0.027	0.033	0.023	0.036
0.008	0.004	0.005	0.010	0.009	0.006	0.013	0.016	0.015	0.009	0.009	0.014
0.000	0.000	0.000	0.000	0.013	0.005	0.000	0.000	0.000	0.000	0.001	0.000
0.000	0.000	0.000	0.000	0.007	0.003	0.000	0.000	0.000	0.000	0.002	0.000
0.008	0.000	0.000	0.003	0.002	0.005	0.000	0.000	0.002	0.000	0.002	0.001
0.008	0.000	0.000	0.004	0.003	0.003	0.000	0.000	0.004	0.000	0.002	0.003
0.006	0.016	0.009	0.011	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.000
0.007	0.008	0.006	0.007	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.000
0.000	0.007	0.003	0.007	0.000	0.001	0.005	0.000	0.000	0.000	0.001	0.000
0.000	0.006	0.004	0.006	0.000	0.002	0.007	0.000	0.000	0.000	0.002	0.000
0.000	0.000	0.000	0.007	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.006	0.002	0.001	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000

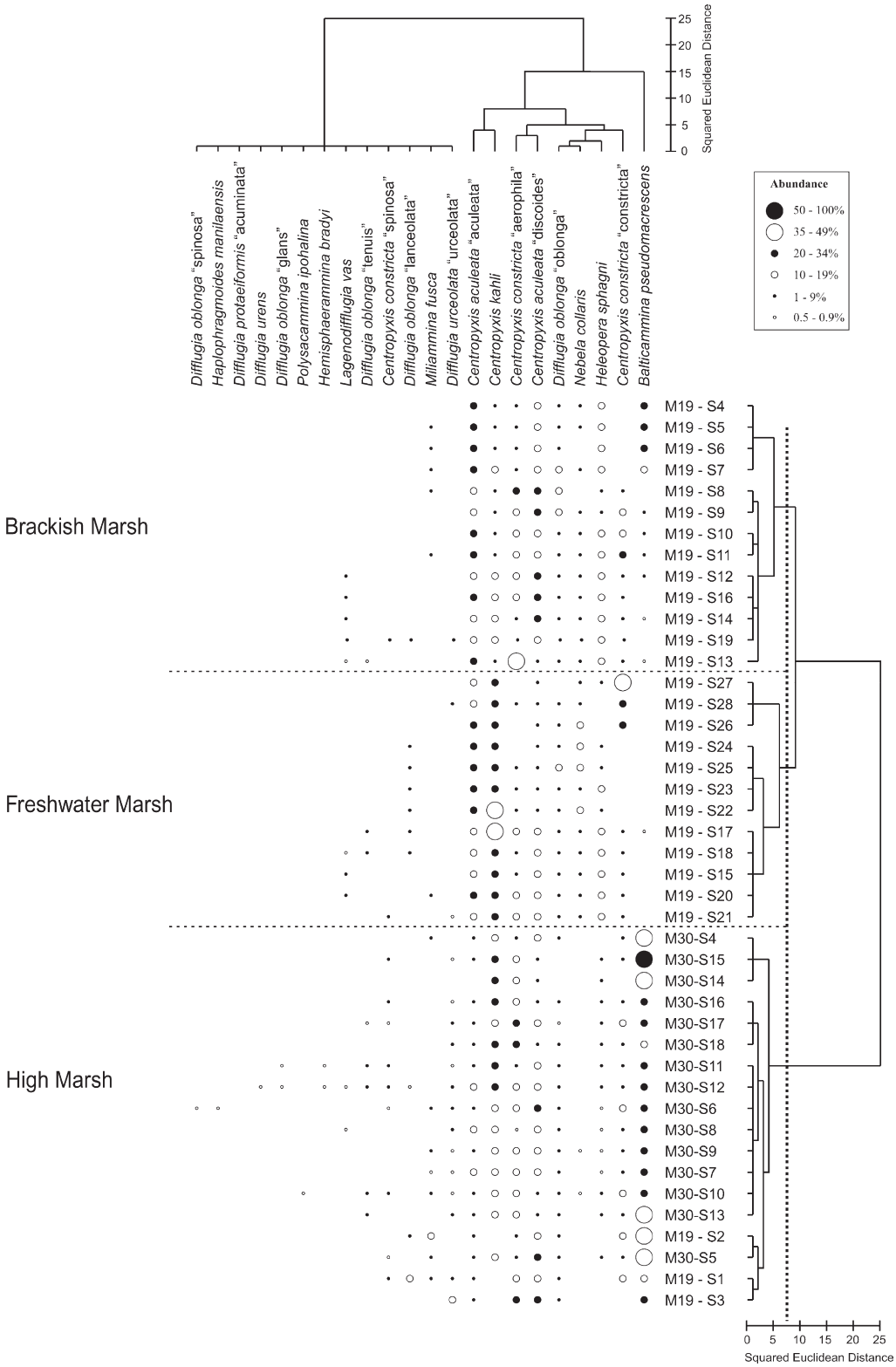

Fig. 3. R-mode vs. Q-mode cluster diagram for sediment samples indicating Freshwater, Brackish and High Marsh Assemblages in WIR12 and WIR16.

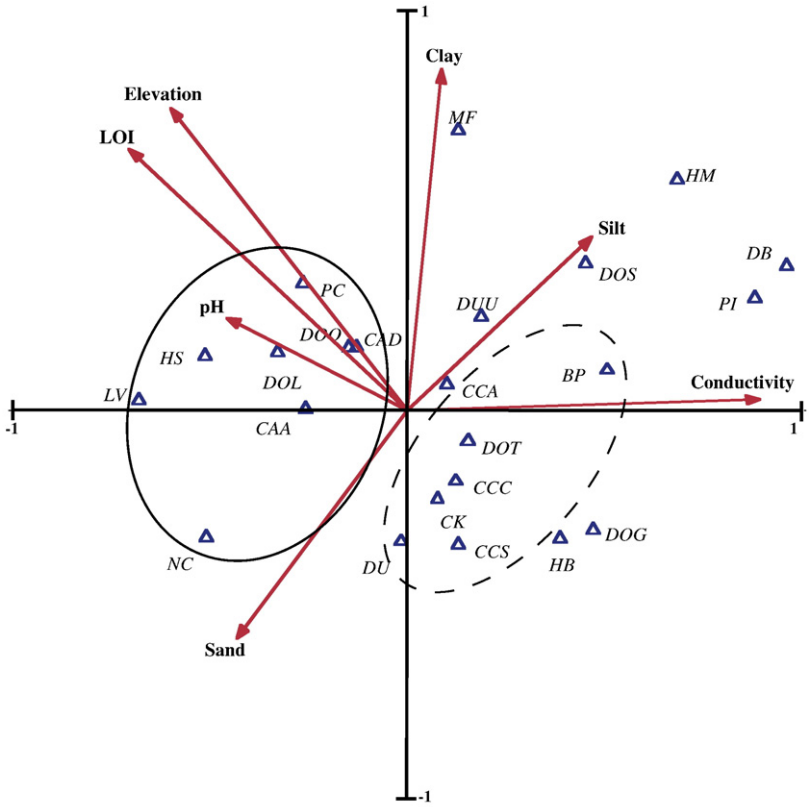

Fig. 4. CCA bi-plot, representing the relation between the faunal distribution in WIR12 and WIR16 and elevation, LOI, conductivity (salinity), clay, silt and sand. The length of the arrows provides an indication of the strength of the correlation. MF: *M. fusca*; HM: *H. manilaensis*; DB: *D. bacillarium*; PI: *P. ipohalina*; DOS: *D. oblonga* "spinosa"; DUU: *D. urceolata* "urceolata"; BP: *B. pseudomacrescens*; CCA: *C. constricta* "aerophila"; PC: *P. compressa*; CAD: *C. aculeata* "discoides"; DOO: *D. oblonga* "oblonga"; DOL: *D. oblonga* "lanceolata"; HS: *H. sphagni*; LV: *L. vas*; CAA: *C. aculeata* "aculeata"; NC: *N. collaris*; DU: *D. urens*; DOT: *D. oblonga* "tenuis"; CCC: *C. constricta* "constricta"; CK: *C. kahli*; CCS: *C. constricta* "spinosa"; HB: *H. bradyi*; DOG: *D. oblonga* "glans". The black circle groups the main species indicative of freshwater and Brackish Assemblages, and the dotted circle indicates the most important species in the High Salt Marsh Assemblage.

(range 0–14.8%, average 8.1%), *C. aculeata* 'discoides' (range 5.5–24.6%, average 12.5%), and *C. aculeata* 'aculeata' (range 0–14.8%, average 7.1%). Small proportions of *D. oblonga* 'oblonga' were also observed (range 0–6.0%, average 2.5%). Although the typically low marsh foraminifera *M. fusca* made up 11.0% of the fauna in one sample, it averaged only 1.4% when measured across all samples of this assemblage. Three other foraminiferal species were also observed albeit in very low numbers: *Hemisphaerammina bradyi* Loeblich and Tappan, 1957, *Haplophragmoides manilaensis* Andersen, 1953 and *Polysaccammina ipohalina* Scott, 1976. The significant presence of freshwater thecamoebians (especially *C. kahli*, but also *H. sphagni* and *Difflugia urceolata* 'urceolata' Reinhardt et al., 1998 in minor quantities) in both the High Marsh and Brackish Assemblages is anomalous.

The dominant species of this assemblage, which includes *B. pseudomacrescens*, *M. fusca*, *D. urceolata* "urceolata", *C. kahli*, and *C. constricta* "constricta", are grouped together by the CCA.

4. Discussion

Although the faunas were similar in both the Waump (WIR16) Marsh in Alison Sound and Wawwat'l (WIR12) Marsh in Seymour Inlet, the succession of observed assemblages identified was different due to elevational disparities between the marshes and the relative salinity at the two sites.

Patterson et al. (2000, 2005) and Guilbault and Patterson (2000) observed a similar relation between assemblages and elevation in the Zeballos Marsh. According to Scott et al. (1980), thecamoebian distribution is

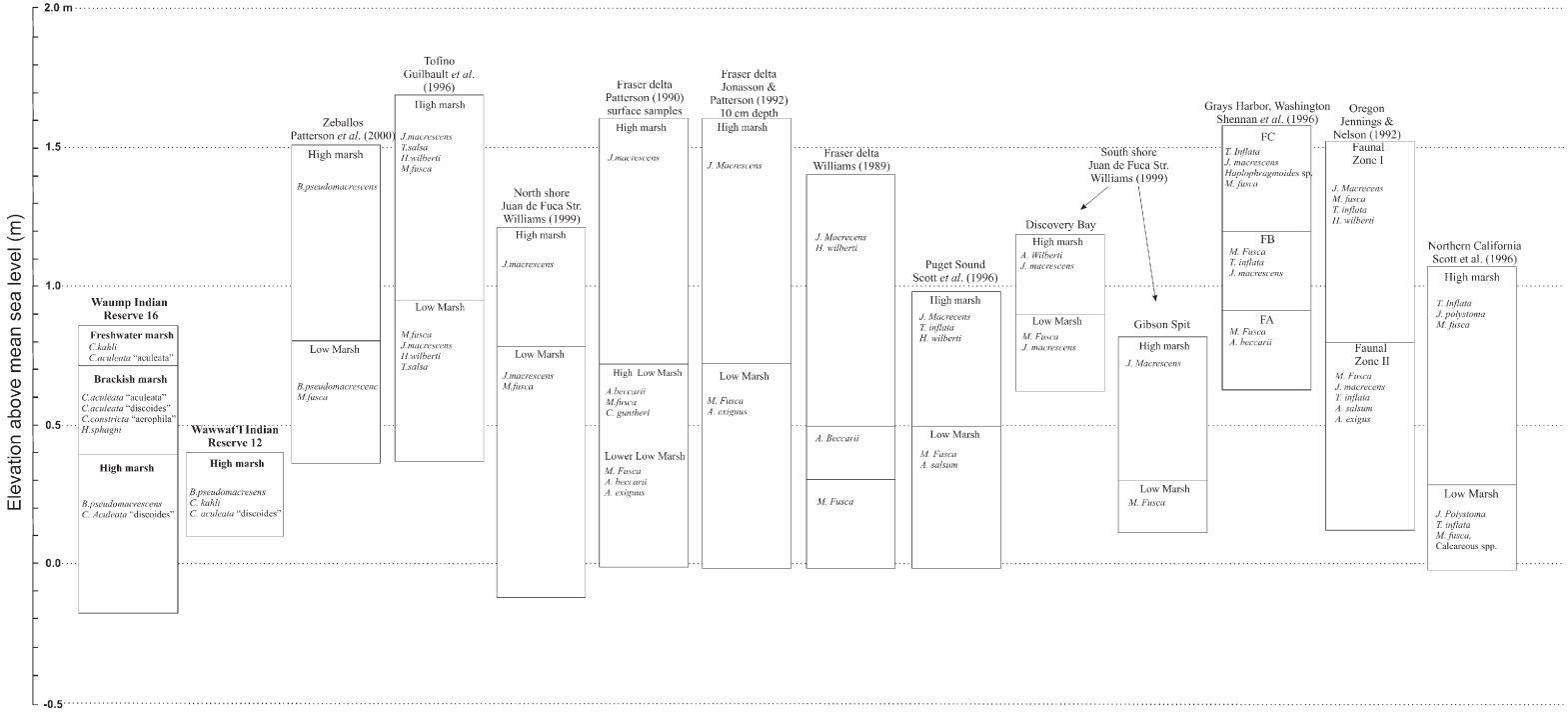

Fig. 5. Summary of foraminiferal and thecamoebian assemblages relative to elevation for marshes in the northwest coast of North America (modified from Williams, 1999).

more heavily influenced by the amount of freshwater influx than elevation. Therefore the high concentrations of testate amoebae in the two transects may reflect periodic freshwater influx from the adjacent streams.

Canonical Correspondence Analysis suggests a major distinction between the terrestrial zone (Freshwater/Brackish) and the high marsh (High Salt Marsh) in the two transects. The results indicate that faunal distribution is strongly related to salinity, and negatively correlated with elevation, LOI and pH. The negative correlation with elevation is also consistent with the distribution pattern of the thecamoebians in both marshes. The High Marsh faunal association is mainly controlled by the inorganic substrate, and longer and more frequent tidal inundation (higher salinity and acidic conditions). In contrast, the Freshwater and Brackish faunal cluster reflect the presence of high organic content in the sediments, and short duration, low frequency tidal inundations (lower salinity and neutral conditions). Axis 2 distinctively identified the impact of sediment types on the species distribution, with species being more abundant in the organic rich clay and silt fractions than in the sand fraction.

Thecamoebians dominate the Freshwater Assemblage of WIR16, especially soil and freshwater species like *C. kahli*, *H. sphagni* and *N. collaris*, which comprise almost 50% of the assemblage. Centropyxids are the other dominant component in this environment, making up ~ 45% of the population. This marsh has a lower salinity (average 2.3‰) and is characterized by a higher riverine input than the WIR12 marsh. The low abundance of foraminifera observed provides further evidence that this part of the marsh is subject to significant saltwater incursions only during storms and spring tides.

The slightly higher salinity Brackish Assemblage, also found in the WIR16 marsh, is primarily dominated by centropyxids (average 56.5%), which along with *D. oblonga*, seem to have a higher salinity tolerance than most other thecamoebian species (Scott et al., 2001). Centropyxids are also known to be opportunist generalists that can survive under stressed conditions including cold temperature (Decloitre, 1956) and low nutrients (Schonborn, 1984), giving them an advantage over other thecamoebians in this harsh marsh ecotone. Other thecamoebian taxa such as *C. kahli*, *H. sphagni* and *N. collaris* still account for one quarter of the observed population though, indicating that they are either able to survive under depressed salinity conditions or are being selectively transported. *B. pseudomacrescens*, an important high salt marsh indicator (De Rijk, 1995; De Rijk and Troelstra, 1997; Gehrels, 1999; Gehrels and van de Plassche, 1999; Patterson et al., 2000), makes its first appearance in this assemblage providing further indication of the transitional nature of this assemblage zone from freshwater to saline conditions. As would be expected in such a transitional environment, the boundary between the Freshwater and Brackish biofacies does not occur at a single elevational point, but is gradational, with an alternation of samples belonging to both assemblages being found between 0.61 and 0.84 m amsl (Fig. 2). Although not employed here, "fuzzy logic models" (Gary et al., 2005) have been applied to continuous variables such as species abundances in stratigraphic data. This approach has great potential in future marsh foraminiferal studies as the transitional area between 0.61 and 0.84 m amsl would be classified neither as belonging to the Freshwater nor Brackish Assemblages, but to both: a concept that agrees more with natural systems than the idea of sudden transitions.

The High Marsh Assemblage comprises most of the WIR12 marsh plus the three lowest samples from WIR16. More than 30% of the observed population is comprised of foraminifera, particularly *B. pseudomacrescens*. An observed abundance of 11% *M. fusca* at −0.09 m amsl in the WIR12 marsh agrees with the sandier substrate present in the sample, suggesting a higher flooding frequency (De Rijk and Troelstra, 1997). This species, though a low salt marsh indicator, may be locally abundant (up to 20%) in high marsh environments (De Rijk and Troelstra, 1997).

The observed distribution of foraminiferal species in this assemblage is in line with the low measured salinity values of 3.3–13.9‰. For example, *H. manilaensis*, a rare species in upper portions of these marshes, made up almost 1% of the assemblage at ~ 0.18 m amsl in WIR12. This species is typically found in lower salinity conditions such as brackish water influenced areas at the rear of marshes, or in low elevation areas associated with fresh water seeps (Parker and Athearn, 1959; Scott and Medioli, 1980; Scott and Leckie, 1990; De Rijk, 1995; De Rijk and Troelstra, 1997; Edwards et al., 2004). The presence of significant proportions (>40%) of thecamoebian species like the soil indicator *C. kahli* (Roe and Patterson, 2006) and centropyxids provide further corroborative evidence of the lower salinity conditions characterizing this assemblage. Although it is possible that many of the observed testate amoebae were transported to the High Marsh during spring freshet episodes, there is evidence that some species may be able to withstand higher levels of salinity than previously thought, including periodic immersion by high tides (Charman et al., 1998). In both marshes studied, the distribution of assemblages are similar to those found on Vancouver Island (Guilbault et al., 1995, 1996; Guilbault and Patterson, 2000;

Patterson et al., 2000), but are displaced seaward due to the higher freshwater influence at WIR12 and WIR16 (Fig. 5). The marshes with a calcareous foraminiferal faunal component on the Fraser River Delta remain anomalous in British Columbia as no calcareous species were found at either WIR12 or WIR16. As has been previously hypothesized by other researchers, the absence of calcareous species is likely due to the harsh, unfavorable environmental low pH, as the presence of low pH in a marsh is not conducive to either the formation or preservation of calcareous foraminiferal tests (Horton, 1999; Patterson et al., 2000), due to the excessive energy required to maintain calcium carbonate. The pH records for these marshes range from measured values of 5.1 in WIR12 marsh to 6.9 in WIR16 marsh (Table 1). Although these values are low enough to inhibit calcareous test formation and preservation, they are sufficiently high for centropyxids to survive. Centropyxids have been demonstrated to diminish at pH levels below 5.5 (Patterson and Kumar, 2002).

5. Conclusions

Three high abundance low diversity foraminifera/thecamoebian dominated assemblages were found to characterize surface transects measured across the marshes at Waump (WIR16) marsh at the head of Alison Sound and Wawwat'l (WIR12) marsh at the head of Seymour Inlet within the Seymour Belize Inlet Complex. The foraminiferal fauna of the High Salt Marsh Assemblage was dominated by *B. pseudomacrescens*, although the significant number of thecamoebians present corroborated measured low salinity values of ≤13.8‰. The transitional Brackish Assemblage, where salinities averaged 2.3‰, was primarily characterized by salinity tolerant centropyxid thecamoebians, and the highest elevation Freshwater Assemblage, where salinities were even lower (average 1.9‰), was dominated by the soil indicator thecamoebian *C. kahli*.

The results of this paper complement previous marsh studies from the region that correlate high salt marsh areas with relative high abundance of *B. pseudomacrescens*. Uppermost intertidal zones identified were defined by thecamoebian assemblages, indicating the importance of including the group in marsh distributional studies, as previously demonstrated in UK marshes (e.g. Charman et al., 2002). The presence of supposedly freshwater thecamoebians in brackish influenced parts of these marshes provides further evidence that there is a wider range of salinity tolerance amongst many of these species than previously thought. Further research on their ecological constraints is required, particularly if they are to be used in marsh-based paleo-sea level research.

This research demonstrates though that an integrated foraminifera/thecamoebian analysis can provide meaningful elevation correlated assemblages, even under low salinity marsh conditions, and provides valuable baseline data for future paleo-sea level reconstruction in these marshes.

Acknowledgements

This work was supported by a Natural Sciences and Engineering Research Council Discovery Grant and Canadian Foundation for Climate and Atmospheric Sciences grant to RTP. Acknowledgement is made to the crew of the CCGS *Vector* for providing security protection against the 34 grizzly bears present in the area during collection of these samples. This paper is a contribution to International Geologic Correlation Programme Project 495; Quaternary Land–Ocean Interactions: Driving Mechanisms and Coastal Responses.

Appendix A

A.1. Systematics of thecamoebians

Subphylum SARCODINA Schmarda, 1871
Class RHIZOPODEA von Siebold, 1845
Subclass LOBOSA Carpenter, 1861
Order ARCELLINIDA Kent, 1880
Superfamily ARCELLACEA Ehrenberg, 1830
Family CENTROPYXIDIDAE Deflandre, 1953
Genus *Centropyxis* Stein, 1859
Centropyxis aculeata (Ehrenberg, 1832)
Strain 'aculeata' Reinhardt et al., 1998
Arcella aculeata Ehrenberg, 1832, p. 91
Centropyxis aculeata 'aculeata' Reinhardt et al., 1998, pl. 1, fig. 1.
Centropyxis aculeata Ehrenberg, 1832
Strain 'discoides' Reinhardt et al., 1998
Arcella discoides Ehrenberg, 1843, p. 139
Arcella discoides Ehrenberg, Ehrenberg, 1872, p. 259, pl. 3, fig. 1
Arcella discoides Ehrenberg, Leidy, 1879, p. 173, pl. 28, figs. 14–38
Centropyxis aculeata var. *discoides* Penard, 1890, p. 150, pl. 5, figs. 38–41
Centropyxis discoides Penard [sic], Odgen and Hedley, 1980, p. 54, pl. 16, figs. a–e
Centropyxis aculeata 'discoides' Reinhardt et al., 1998, pl. 1, fig. 2

Centropyxis constricta (Ehrenberg, 1843)
Strain 'constricta' Reinhardt et al., 1998
Arcella constricta Ehrenberg, 1843, p. 410, pl. 4, fig. 35, pl. 5, fig. 1
Centropyxis constricta 'constricta' Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 1, fig. 4
Centropyxis constricta (Ehrenberg, 1843)
Strain 'aerophila' Reinhardt et al., 1998
Centropyxis aerophila Deflandre, 1929
Centropyxis aerophila Deflandre, Odgen and Hedley, 1980, p. 48–49
Cucurbitella [sic.] *constricta* Reinhardt et al., 1998, pl. 1, fig. 6
Centropyxis constricta (Ehrenberg, 1843)
Strain 'spinosa' Reinhardt, Dalby, Kumar and Patterson, 1998
Centropyxis spinosa CASH in Cash and Hopkinson, 1905, p. 135, text figs. 26 a–c, pl. 16, fig. 15
Centropyxis spinosa Cash, Odgen and Hedley, 1980, p. 62, pl. 20, figs. a–d.
Genus *Cyclopyxis* Deflandre, 1929
Cyclopyxis kahli (Deflandre, 1929)
Centropyxis kahli Deflandre, 1929, p. 330
Cyclopyxis kahli (Deflandre) Odgen and Hedley, 1980, p. 70–71, pl. 24, figs. a–e.
Family HYALOSPHENIIDAE Schulze, 1877
Genus *Heleopera* Leidy, 1879
Heleopera sphagni (Leidy, 1874)
Difflugia sphagni Leidy, 1874, p. 157
Heleopera picta Leidy, 1879
Heleopera sphagni (Leidy) Medioli and Scott, 1983, p. 37–38, pl. 6, figs. 15–18
Genus *Nebela* (Leidy, 1874)
Nebela collaris (Ehrenberg, 1848)
Nebela collaris Ehrenberg, 1848
Nebela collaris Ehrenberg, Odgen and Hedley, 1980, p. 94–95
Family DIFFLUGIDAE Stein, 1859
Genus *Difflugia* Leclerc in Lamarck, 1816
Difflugia oblonga Ehrenberg, 1832
Strain 'glans' Reinhardt et al., 1998
Difflugia glans Penard, 1902
Difflugia oblonga 'glans' Reinhardt et al., 1998, pl. 2, fig. 7
Difflugia oblonga Ehrenberg, 1832
Strain 'lanceolata' Reinhardt et al., 1998
Difflugia lanceolata Penard, 1890, p. 145, pl. 4, figs. 59–60
Difflugia lanceolata Penard, Odgen and Hedley, 1980, p. 140, pl. 59, figs. a–d
Difflugia oblonga 'lanceolata' Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 2, fig. 6
Difflugia oblonga Ehrenberg, 1832
Strain 'oblonga' Reinhardt et al., 1998
Difflugia oblonga Ehrenberg, 1832, p. 90
Difflugia oblonga Ehrenberg, Odgen and Hedley, 1980, p. 148, pl. 63, figs. a–c
Difflugia oblonga Ehrenberg, Haman, 1982, p. 397, Pl. 3, figs. 19–25
Difflugia oblonga Ehrenberg, Scott and Medioli, 1983, p. 818, figs. 9a–b
Difflugia oblonga 'oblonga' Reinhardt et al., 1998, pl. 2, fig. 10
Difflugia oblonga Ehrenberg, 1832
Strain 'spinosa' Reinhardt et al., 1998
Difflugia oblonga 'spinosa' Reinhardt et al., 1998, pl. 2, fig. 11
Difflugia oblonga Ehrenberg, 1832
Strain 'tenuis' Reinhardt et al., 1998
Difflugia pyriformis var. *tenuis* Penard, 1890, p. 138, pl. 3, figs. 47–49
Difflugia oblonga 'tenuis' Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 2, fig. 12
Difflugia protaeiformis Lamarck, 1816
Strain 'acuminata' Reinhardt et al., 1998
Difflugia protaeiformis Lamarck, 1816, p. 95
Difflugia acuminata Ehrenberg, 1830, p. 95
Difflugia pyriformis 'claviformis' Penard, 1899, p. 25, pl. 2, figs. 12–14.
Difflugia claviformis Ehrenberg, Odgen and Hedley, 1980, p. 126, pl. 52, figs. a–d.
Difflugia acuminata Ehrenberg, Scott and Medioli, 1983, p. 818, fig. 9d.
Difflugia protaeiformis 'claviformis' Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 2, fig. 3.
Difflugia urceolata Carter, 1864
Strain 'urceolata' Reinhardt et al., 1998
Difflugia urceolata Carter, 1864, p. 27, pl. 1, fig. 7
Difflugia urceolata Carter, Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 2, fig. 2b
Difflugia urens Patterson et al., 1985
Difflugia urens Patterson et al., 1985, p. 130, pl. 3, figs. 5–14
Genus *Lagenodifflugia* Medioli and Scott, 1983
Lagenodifflugia vas (Leidy, 1874)
Difflugia vas Leidy, 1874, p. 155
Lagenodifflugia vas Leidy, Medioli and Scott, 1983, p. 33, pl. 2, figs. 18–23, 27, 28
Lagenodifflugia vas Leidy, Reinhardt, Dalby, Kumar and Patterson, 1998, pl. 1, fig. 8
Genus *Pontigulasia* Rhumbler, 1895
Pontigulasia compressa (Carter, 1864)
Difflugia compressa Carter, 1864, p. 22, pl. 1, figs. 5–6

Pontigulasia compressa Carter, Medioli and Scott, 1983, p. 35–36, pl. 6, figs. 5–14

A.2. *Systematics of Foraminifera*

Order FORAMINIFERIDA Eichwald, 1830
Family RZEHAKINIDAE Cushman, 1933
Genus *Miliammina* Heron-Allen and Earland, 1930
Miliammina fusca (Brady, 1870)
Quinqueloculina fusca BRADY, in Brady and Robertson, 1870, p. 286, pl. 11, fig. 2.
Miliammina fusca (Brady) Patterson, 1990, p. 240, pl. 1, fig. 4.
Family POLYSACCAMMINIDAE Loeblich and Tappan, 1984
Subfamily POLYSACCAMMININAE Loeblich and Tappan, 1984
Genus *Polysaccammina* Scott, 1976
Polysaccammina ipohalina Scott, 1976
Polysaccammina ipohalina Scott, 1976, p. 319, 320, text figure 4, pl. 2, figs. 1–4.
Family HEMISPHAERAMMINIDAE Loeblich and Tappan, 1961
Subfamily HEMISPHAERAMMININAE Loeblich and Tappan, 1961
Genus *Hemisphaerammina* Loeblich and Tappan, 1957
Hemisphaerammina bradyi Loeblich and Tappan, 1957
Hemisphaerammina bradyi Loeblich and Tappan in Loeblich and Collaborators, 1957, p. 224, pl. 72, fig. 2; Scott et al., 1977, p. 1579, pl. 3, figs. 7, 8.
Crithionina pisum Goes. Gregory, 1970, p. 165, pl. 1, fig. 6.
Hemisphaerammina sp. Cole and Ferguson, 1975, pl. 1, fig. 4.
Family TROCHAMMINIDAE Schwager, 1877
Subfamily POLYSTOMAMMININAE Brönnimann and Beurlen, 1977
Genus *Balticammina* Brönnimann, Lutze, and Whittaker, 1989
Balticammina pseudomacrescens Brönnimann, Lutze, and Whittaker, 1989
Trochammina macrescens Lutze, 1968, p. 25–26, table 1, fig. 9; Scott and Medioli, 1980, p. 44–45, pl. 3, figs. 1–3.
Trochammina inflata (Montagu) var. *macrescens* Scott, 1976, p. 320, pl. 1, figs. 4–7; Scott, Medioli, and Schaffer, 1977, p. 1579, pl. 4, figs. 6, 7.
Trochammina macrescens (Type A) De Rijk, 1995, pl. 1, figs. 1–3.
Trochammina macrescens macrescens Scott et al., 1990, p. 733, pl. 1, figs. 1a, b.
Balticammina pseudomacrescens Brönnimann, Lutze, and Whittaker, 1989, p. 169, pl. 1–3.
Family HAPLOPHRAGMOIDIDAE Maync, 1952
Genus *Haplophragmoides* Cushman, 1910
Haplophragmoides manilaensis Andersen, 1953
Haplophragmoides manilaensis Andersen, 1953, p. 22, pl. 4, figs. 8a–b; Patterson, 1990, p. 239, pl. 2, figs. 3, 6; Jonasson and Patterson, 1992, p. 297, pl. 1, fig. 2

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